
POLLINATION OF *MORAEA* SPECIES (IRIDACEAE) WITH A STAMINAL COLUMN¹

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ABSTRACT

The ancestral and most common flower in the African genus *Moraea* is *Iris*-like and consists of three functional units (meranthia). Each unit consists of an outer tepal opposed to a broad style branch terminating in prominent paired crests, together forming a gullet-like unit. However, many species in this genus of some 200 species have mechanically protandrous flowers in which the three stamens form a sheath surrounding the style and the style branches are narrow, with reduced stigmatic crests, and the subequal inner and outer tepal whorls form a shallow or deep bowl sometimes fully enclosing the stamens and style branches. The flowers secrete hexose-dominant nectar and, except for *M. collina*, are self-incompatible. Flowers of the nine species in two sections studied comprise two different modes of pollination based on the presentation of the staminal column and perianth, pigmentation, scent, and edible rewards. In five species, *M. collina*, *M. comptonii*, *M. elegans*, *M. ochroleuca*, and *M. vallisbelli*, the perianth forms a wide or narrow bowl and produces strong, sweet or musk-like odors, and the weakly diverging anthers are appressed to the narrow, inconspicuous style branches. These flowers are pollinated primarily by flower flies, scarab beetles, and honey bees that land on the perianth and brush against the anthers and/or receptive stigmas while foraging for nectar or pollen, or in the case of beetles merely assembling on the flowers. In the second group of species, *M. bifida*, *M. miniata*, *M. pseudospicata*, and *M. reflexa*, the perianth is stellate, pink, yellow, or blue, usually without discernable scent, the filaments are united into a column that is exerted from the flower, and the anthers are usually coherent. These flowers are pollinated primarily by polylectic bees in the families Apidae (*Anthophora diversipes*, *Apis mellifera*) and Melittidae (*Rediviva* spp.). The bees land on the staminal column and forage for pollen, sometimes later moving onto the perianth to take nectar present at the base of the tepals. The columns of these species are interpreted as both morphological and functional intermediates between pollen presenters or protostigmas (e.g., in Asterales, Campanulales, Proteales) and true gynostemium/gynostegia (in Asclepiadaceae, Orchidaceae, and Stylidiaceae). These flowers represent a profound shift in the ancestral pollination strategy in the genus from one of passive pollen deposition on bees foraging for nectar on meranthia to one of active foraging for nectar or pollen on whole flowers.

Floral morphology in the Iridaceae is usually closely correlated with the diversity of pollinators. For example, most species in the genera *Lapeirousia* and *Nivenia* have flowers with elongated floral tubes and are pollinated by nemestrinid and tabanid flies and sphinx moths that have probosces longer than their bodies and often forage for nectar while hovering (Vogel, 1954; Goldblatt & Bernhardt, 1990; Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997). Conversely, North American *Sisyrinchium* species, and some species of the southern African genera, including *Aristea*, *Ixia*, *Romulea*, and *Sparaxis*, have stellate or rotate perianths, the latter with reduced, often non-functional floral tubes. The primary pollinators of these flowers include small- and large-bodied bees, large scarab beetles (Hopliinae), and short-tongued flies that must land on the tepals to collect nectar and/or

pollen (Henderson, 1976; Cholewa & Henderson, 1984; Goldblatt et al., 1998a; Goldblatt & Manning, 1997). In southern Africa scarab beetles also use the flowers as sites for assembly and mating. Genera pollinated primarily by large bees with long probosces (e.g., *Gladiolus*) have zygomorphic, bilabiate flowers in which the lower tepals form a landing platform (Vogel, 1954; Goldblatt et al., 1998b).

In *Iris* and most species of *Moraea* the individual flowers comprise three functionally separate pollination units, or meranthia (Faegri & van der Pijl, 1979). Each meranthium resembles a bilabiate gullet flower and consists of a large outer tepal, the claw of which is closely opposed to a flattened style branch that bears a transverse stigma and terminal, petal-like crests (Fig. 1). The major pollinators are large bees that land on the outer tepal limb and

¹ Support for this study by grant 5408-95 from the National Geographic Society is gratefully acknowledged. We thank H. Dombrow, Wurms, Germany, D. Barraclough, KwaZulu-Natal Museum, Pietermaritzburg, and V. Whitehead, South African Museum, Cape Town, for identification of insects, and B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for the nectar analyses.

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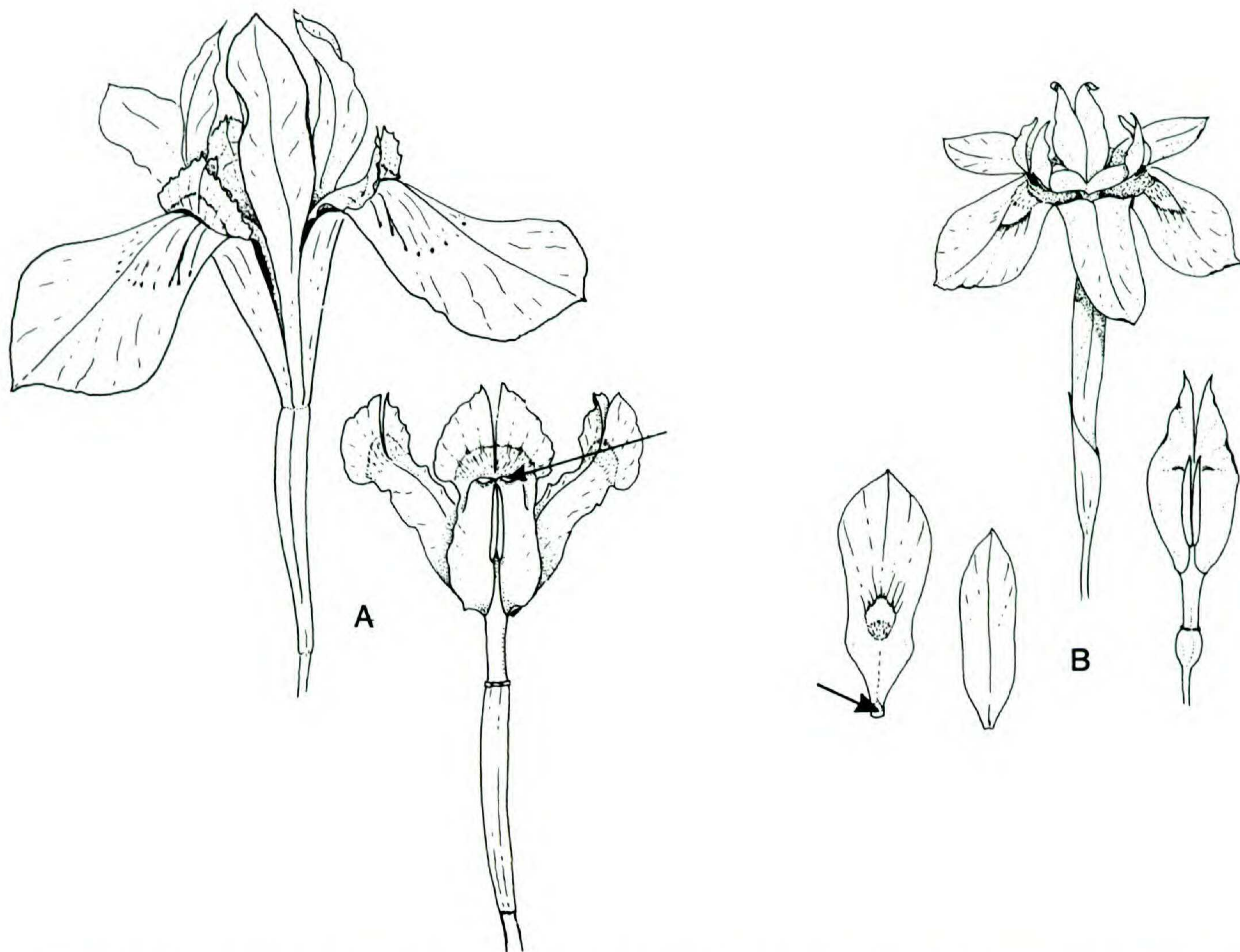


Figure 1. Classic *Iris*-type flower of *Moraea*. —A. *M. huttonii* (Baker) Oberm., with stamens and style branch enlarged and arrow indicating the stigmatic lobes of one style branch. —B. *M. inclinata* Goldblatt, with one stamen and the opposed style branch and an inner and outer tepal enlarged with arrow indicating position of perigonal nectary. Whole flowers $\times 1.5$, dissections much enlarged. Drawn by Margo Branch.

push their bodies between the style branch and tepal claw to forage for nectar (Müller, 1883; Goldblatt et al., 1989; Proctor et al., 1996).

Among the southern African species of *Moraea*, now including *Homeria* and *Hexaglottis* (Goldblatt, 1998), there are some striking modifications to the ancestral flower (Goldblatt, 1981, 1986). Some 60 species of the genus belonging to several different lineages have flowers in which the three-part, bilabiate form has been lost. Style crests are reduced or absent, filaments form a column, anthers are often coherent, and the outer whorl of tepals does not differ from the inner whorl at all in orientation and hardly in size and shape. In these flowers the tepal claws are not associated with the style branches to form a floral throat or gullet (Figs. 2, 3). These floral forms suggest alternative pollination systems. Here we examine nine representative species with these flowers and compare them with what is known of pollination in the remaining species of *Moraea* and other Iridaceae specifically, and within the angiosperms in general.

METHODS

Field studies were conducted in the winter-rainfall zone of southern Africa over the past 25 years as opportunity arose while in the course of research on the systematics of various genera of the Iridaceae (Table 1). Observation of insect foraging involved 4–10 hours per plant species and included recording of floral attractants (pigment patterns, scent, nectar), the behavior of insects on the flower, and the taxonomic diversity of floral foragers. Casual observations made in other years have confirmed many of the observations reported for particular study sites. Flower visitors were captured if they were seen to contact the sexual organs of the flower or while they foraged for floral nectar and/or pollen. Netted insects were killed in a jar using ethyl acetate fumes. To prevent contamination with pollen carried by another insect in the killing jar, specimens were isolated from each other by wrapping them in tissue. Insect length was measured from the pronotum to the posterior tip of the abdomen.

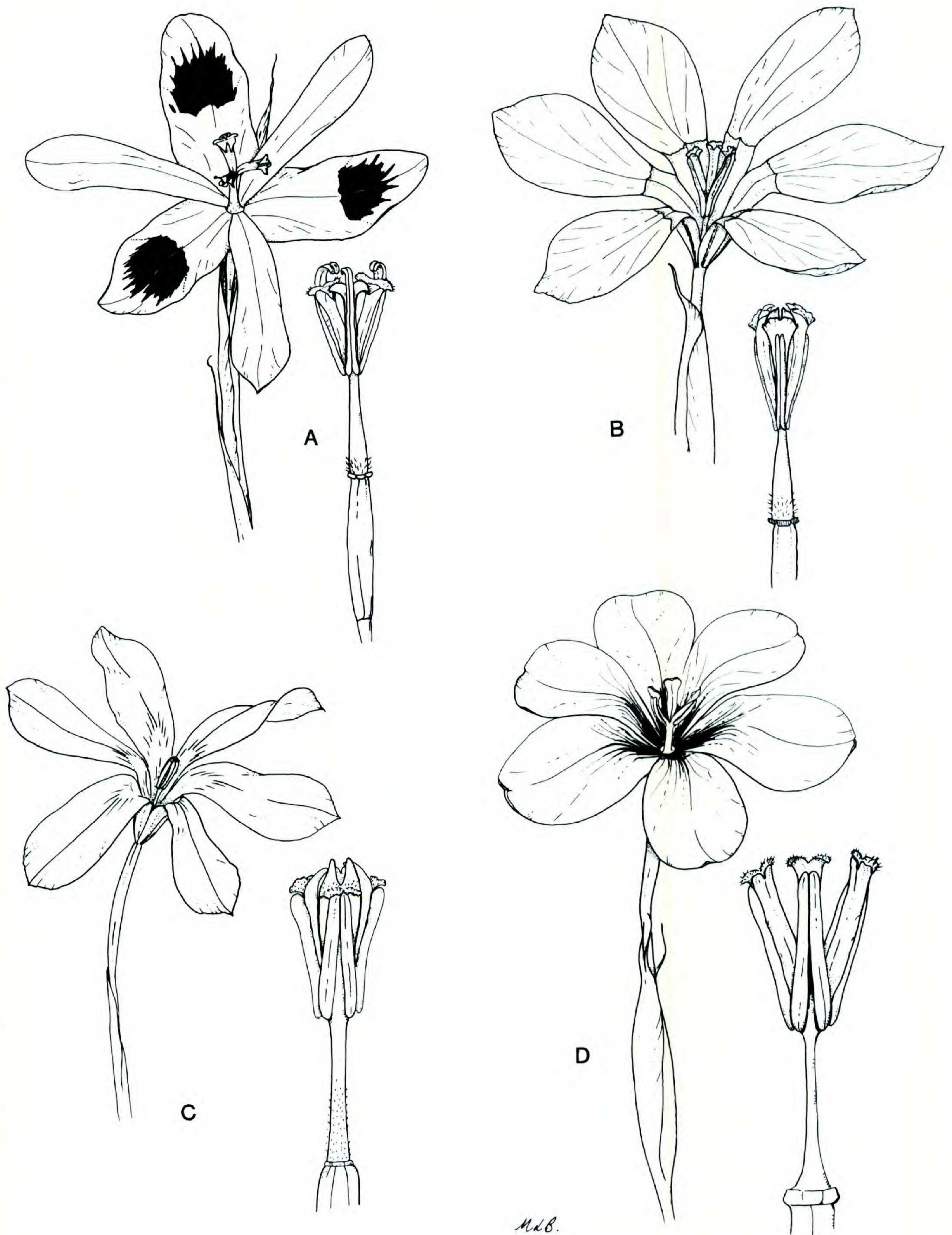


Figure 2. Bowl flowers of *Moraea* species studied with detail of the stamen–style branch unit. —A. *Moraea elegans*. —B. *M. comptonii*. —C. *M. collina*. —D. *M. ochroleuca*. Whole flowers $\times 1.5$, stamen–style unit much enlarged. Drawn by Margo Branch.

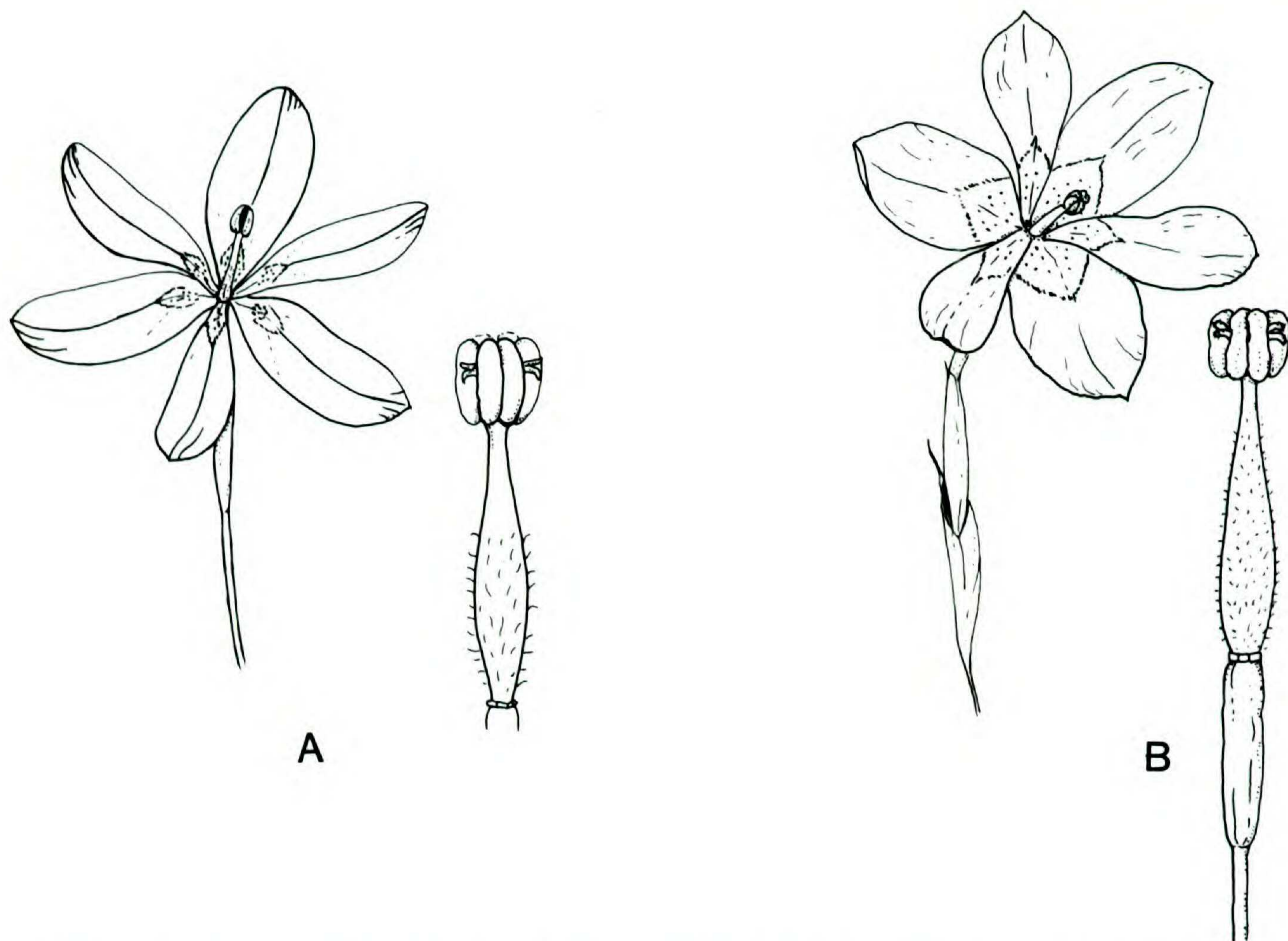


Figure 3. Stellate flowers of *Moraea* species studied with detail of the stamen–style branch unit. —A. *Moraea miniata*. —B. *M. bifida*. Whole flowers $\times 1.5$, stamen–style unit much enlarged. Drawn by Margo Branch.

Pollen was removed from insects by placing the pinned specimen on a glass slide and either scraping pollen off the body with a dissecting needle or gently washing the specimen in drops of 95% ethanol. The residue from needle probes or washes was collected on glass slides and mounted in 1–2 drops of Calberla's fluid (Ogden et al., 1974). Pollen was scored as present on an insect if more than 10

grains (or polyads) were observed on the slide (Table 4). Pollen grains were identified by comparison with a reference set of pollen preparations made from plants flowering at study sites.

Insects were identified by H. Dombrow, Wurms, Germany (beetles), D. Barraclough, KwaZulu-Natal Museum, Pietermaritzburg (most Diptera), and V. Whitehead, South African Museum, Cape Town

Table 1. Research sites and voucher data for species studied. All localities are in Western Cape Province, South Africa. All vouchers are deposited at MO.

Species	Locality	Voucher
<i>M. bifida</i> (L. Bolus) Goldblatt	Nieuwoudtville, Glenlyon Estate, Aug. 1976, and Sep. 1996	Goldblatt 3969
<i>M. collina</i> Thunb.	Cape Town, Signal Hill, Aug. 1996	Goldblatt s.n. (no voucher)
<i>M. comptonii</i> (L. Bolus) Goldblatt	Near Bot River, Aug. 1997	Goldblatt 3997
<i>M. elegans</i> Jacq.	Napier, Fairfield Estate, Aug.–Sep. 1996	Goldblatt 10255
<i>M. miniata</i> Andr.	Near Clanwilliam, Sep. 1996	Goldblatt 2563
<i>M. ochroleuca</i> (Salisb.) Drapiez	Foot of Sir Lowry's Pass, Aug. 1996	Goldblatt 10248
<i>M. reflexa</i> Goldblatt	Cape Peninsula, near Kommetje, July 1976	Goldblatt 3615
<i>M. vallisbellii</i> (Goldblatt) Goldblatt	Calvinia, top of Hantamsberg, Oct. 1995	Goldblatt 10555
<i>M. pseudospicata</i> Goldblatt	West of Nieuwoudtville, Oct. 1996	Goldblatt 4032
	Nieuwoudtville Wild Flower Reserve, Apr. 1997	Goldblatt 10797

Table 2. Floral characteristics of species of *Moraea* studied, including shape, perianth color and marking, presence of nectar, and flowering time. Abbreviations: + = presence, - = absence.

	Flower		Scent	Nec- tar	Flowering time	Floral longevity
	Shape	Color				
<i>Moraea</i> sect. <i>Homeria</i>						
<i>M. bifida</i>	star	pink	-	+	Sep.-Oct.	ca. 12-5 PM (ca. 6 hr.)
<i>M. collina</i>	bowl	yellow or pink	+	+	Aug.-Sep.	ca. 12-4 PM, 2 days (ca. 36 hr.)
<i>M. comptonii</i>	bowl	yellow or pink	+	+	Aug.-Sep.	10 AM-4 PM, 2 days (30 hr.)
<i>M. elegans</i>	bowl	yellow	+	+	Sep.	10 AM-5 PM, 2 days (30 hr.)
<i>M. miniata</i>	star	pink (or yellow)	-	+	Sep.	1-6 PM (ca. 5 hr.)
<i>M. ochroleuca</i>	bowl	yellow	+	+	Aug.-Oct.	10 AM-5 PM, 2 days (ca. 30 hr.)
<i>M. reflexa</i>	star	yellow	+	+	Oct.	1 day (ca. 6 hr.)
<i>M. vallisbelli</i>	bowl	yellow or pink	-	+	Sep.-Oct.	11 AM-4 PM (ca. 6 hr.)
<i>Moraea</i> sect. <i>Polyanthes</i>						
<i>M. pseudospicata</i>	star	blue	-	+	Mar.-Apr.	ca. 3:30-6 PM (2.5 hr.)

(*Rediviva* bees). Plant voucher specimens have been deposited at the Missouri Botanical Garden (MO), and insects at the KwaZulu-Natal and South African Museums. Bee taxonomy followed is that of Roig-Alsina and Michener (1993).

The presence of nectar was determined in the field by withdrawing nectar from the base of the floral tube with 2- μ l capillary tubes after separating the ovary from the perianth. When volumes were too small to sample in the field, stems were cut and placed in water and nectar was sampled in the laboratory within 18 to 24 hours. Experience showed that nectar characteristics gradually change in *Moraea* species if stems are retained in water for longer periods. Volume and solute content are based on laboratory measurements of flowers of plants maintained in water (Table 3). Nectar samples were dried on Whatman's filter paper no. 1 and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for HPTCL analysis (Table 3). The percentage of sugars dissolved in fresh nectar (Table 3) was recorded on a Bellingham & Stanley hand-held refractometer (0-50%) using nectar extracted from flowers in the manner described above. When volumes were too small to measure or to determine sugar concentration, the presence of nectar was estimated by brushing nectariferous areas of flowers against the tongue.

Floral scent was noted in the field and in cultivated plants. Flowers of species with scents too weak to be discerned by the human nose were recorded after individual flowers were picked and placed in clean, lidded glass jars and stored in a warm place. The contents of each jar was smelled after a minimum of 60 minutes (Buchmann, 1983).

Compatibility was determined in the greenhouse by self- or cross-pollinating emasculated flowers.

Sufficient pollen was applied to the stigma to be visible to the naked eye. Two types of pollination were made. One: cross-pollinations of at least five emasculated flowers received pollen from a second genotype of the same species. Two: self-pollinations of at least five emasculated flowers each received pollen of the same genotype.

RESULTS

Floral phenology and habit. Species studied are corm-bearing, seasonal geophytes native to the winter-rainfall region of southern Africa, that is, the southern and western coast and near interior of the subcontinent. Eight species bloom from late winter to mid spring, while *M. pseudospicata* blooms in the autumn (Table 2). All nine species typically form clumped populations with over five individuals per square meter not uncommon and with each flowering shoot bearing two to four open flowers per day.

Flowers last one or two days depending on the species. One-day flowers usually last 6-8 hours, but only 2.5 hours in *M. pseudospicata*. Flowering is strongly synchronized. On some days no flowers are produced in a population and on other days most individuals with flowering stems produce flowers. The time of flower opening is species specific (Table 2). The flowers of *Moraea collina*, *M. comptonii*, *M. elegans*, and *M. ochroleuca* close in the late afternoon and reopen on the following day, withering by late afternoon.

The flowers of all nine species show morphological protandry. That is, anthers dehisce within one hour after tepals expand but stigmatic surfaces remain folded against opposed stylar tissue for at least 2 hours in those species in which flowers last a single day. In *M. collina*, *M. comptonii*, and *M.*

Table 3. Nectar characteristics of species studied. Nectar analyses were provided by B.-E. van Wyk, Rand Afrikaans University, Johannesburg, South Africa (n = number of individuals sampled).

Species	Nectar		Sugar ratios %			Sucrose/ F + G (n)
	Volume μL (n)	Conc. % (\pm SD)	Fru	Glu	Suc	
<i>M. bifida</i>	trace amount present		50–51	49–50	0	0 (2)
<i>M. collina</i>	0.2–0.6 (4)	47.8 (2.1)	47–52	48–53	0	0 (4)
<i>M. reflexa</i>	2.5–5.0 (2)	9.0–12.0	50.5	49.5	0	0 (2)
<i>M. ochroleuca</i>	trace amount present		49–50	50–51	0	0 (2)

elegans the stigmas are not exposed until the mid afternoon of the first day of flowering, and in *M. ochroleuca* not until the second day of the floral lifespan.

Floral compatibility. *Moraea collina* was the only species that set seed following self-pollination. All remaining species were strongly self-incompatible, as no capsules were produced after at least five hand self-pollinations; full capsules were produced by cross pollinations. Flowers of *M. collina* are thus self-compatible and are in addition weakly autogamous, as shown by flowers of greenhouse-grown plants that were not hand pollinated.

Floral presentation and rewards. Flowers of *Moraea* species are produced in several-flowered monochasial cymose inflorescences (rhipidia) with the buds enclosed until the day before anthesis in a pair of large, green, leathery sheathing bracts (spathes) (Goldblatt, 1986, 1990). Flowers are actinomorphic and are produced sequentially from a rhipidium 1–3 days apart during the flowering season, when they are exerted from the spathes as the pedicels elongate.

Flowers are of two contrasting forms (Table 2). In the first (Fig. 2), the tepals have elongated, ascending claws forming a narrow to wide bowl while the tepal limbs spread horizontally. The perianths are either yellow or pale salmon pink, but other species (not included in this study) may have blue or white flowers, e.g., *M. polyanthos* L.f. Flowers are usually uniformly colored within a population, but at our study site for *M. comptonii* plants had either yellow or salmon flowers, and some populations of this species have green markings on the outer or all tepals. Individuals of *M. vallisbelli* also may have yellow or pink flowers within a population. Pale yellow nectar guides, typically outlined in dark gray, are usually present at the base of the tepal limbs, but *M. ochroleuca* has no visible nectar guides (Fig. 2D), although some individuals have the floral cup a deeper shade of yellow. Flowers of *M. elegans* have prominent, large, dark green and

or orange markings on the distal halves of the outer tepals (Fig. 2A).

The bowl-shaped flowers are typically scented, with odors reminiscent of musk (*M. ochroleuca*), honey (*M. collina*), or fruity odors with a strong component of coconut (*M. comptonii*, *M. elegans*). The united filaments enclose the style, and the weakly divergent anthers are appressed to narrow style branches. The style branches reach to the middle or just beyond the anther tips and have terminal, bilobed stigmatic surfaces. The staminal column and the style branches are included in the floral bowl, but barely so in *M. comptonii* and *M. elegans* in which the bowl is wide and shallow.

In the second floral type (Fig. 3) the tepal claws are short and erect while the limbs spread horizontally or are reflexed. The perianth is thus more or less stellate. The perianths are usually pink, sometimes yellow or blue, but are typically uniformly colored within populations. *Moraea reflexa* always has yellow flowers, and *M. pseudospicata* blue flowers (Table 2). Yellow nectar guides, often with minute blackish dots, are present at the base of the tepal limbs. Only *M. reflexa* has flowers that produce a light sweet odor. None of the remaining species with stellate flowers produces a discernible scent even when kept in lidded glass jars. In these flowers the stamens form an elongated, and disproportionately prominent column with the fused filaments enclosing the style and the anthers either diverging (*M. reflexa*) or coherent (Fig. 3). The filament column is smooth and slender (*M. pseudospicata*) or lightly papillate and inflated and bulbous above the base. When the filament column is bulbous a small chamber is formed between the tepal claws and lower portion of the column. The staminal column is well exerted from the flower, and the anthers and pollen are prominently displayed. When the anthers are contiguous the stigmatic tips of the style branches emerge between the anthers after anther dehiscence (Fig. 3), and in the field are usually visible after pollen has been removed from the anthers by insect visitors. Pollen and stigmatic

Table 4. Pollen load analysis of collected beetles. Taxonomic affiliations are as follows: Coleoptera: *Anisochelus*, *Anisonyx*, *Peritrichia*, *Platychelus* (Scarabaeidae). Diptera: *Anthomyia* (Anthomyiidae); *Orthellia* (Muscidae); *Scathophaga* (Scathophagidae). Hymenoptera–Apoidea: *Andrena* (Andrenidae); *Anthophora* (Anthophoridae); *Apis* (Apidae); *Lasioglossum*, *Patellapis* (Halictidae); *Rediviva* (Melittidae).

Plant and insect taxon	Number of insects carrying pollen loads of:			
	Host flr only	Host flr + other sp.	Other sp. only	No pollen
Bowl flowers:				
<i>M. collina</i>				
<i>Anisonyx ursus</i>	3	0	0	0
<i>Apis mellifera</i>	0	4	0	0
<i>Lasioglossum pearstonensis</i>	0	0	3	4
<i>Patellapis</i> sp.	0	3	0	1
<i>M. comptonii</i>				
<i>Apis mellifera</i>	0	3	0	0
<i>Anthophora diversipes</i>	0	2	0	0
<i>Orthellia</i> sp.	5	0	0	0
<i>Platychelus</i> sp.	2	2	0	0
<i>M. elegans</i>				
<i>Apis mellifera</i>	2	0	0	0
<i>Orthellia</i> sp.	0	2	0	1
<i>Peritrichia pseudoplebia</i>	7	2	0	1
<i>Scathophaga stercoraria</i>	0	0	0	3
<i>M. ochroleuca</i>				
<i>Anisonyx ursus</i>	2	0	0	0
<i>Anthomyia</i> sp.	0	0	0	1
<i>Apis mellifera</i>	3	1	0	0
Calliphoridae	0	0	1	0
<i>Orthellia</i> sp.	10	0	0	0
<i>Musca</i> sp.	0	2	0	1
<i>Scathophaga stercoraria</i>	0	2	0	3
Syrphidae	0	1	0	0
<i>M. vallisbelli</i>				
<i>Anisochelus inarmatus</i>	6	5	0	2
	40	29	4	17
Stellate flowers:				
<i>M. bifida</i>				
<i>Apis mellifera</i>	0	3	0	0
<i>Rediviva macgregorii</i>	0	2	0	0
<i>M. miniata</i>				
<i>Apis mellifera</i>	0	3	0	0
<i>Rediviva parva</i>	0	3	0	0
<i>Rediviva longimanus</i>	0	1	0	0
<i>Anthophora diversipes</i>	0	3	0	0
<i>M. pseudospicata</i>				
<i>Apis mellifera</i>	5	2	0	0
Halictidae	1	1	0	1
<i>M. reflexa</i>				
<i>Apis mellifera</i>	2	0	0	0
	6	18	0	1

surfaces are, however, in close proximity during anthesis, and pollen inevitably comes into contact with stigmatic surfaces unless removed by insect visitors.

Nectar. A small nectar gland (perigonal nectary) is located at the base of each tepal in seven species but only at the base of the outer tepals in *Moraea comptonii* and *M. elegans*. In species with bowl-shaped flowers nectar droplets are visible after flowers open. Discrete nectar glands are not present in *M. ochroleuca*, but nectar is secreted over the lower surface of the tepals above vascular traces, visible as darker streaks on the tepals. Nectar is concealed between the tepal claws and filament column in a small nectar chamber in species with stellate flowers. In all nine species nectar is available in such small quantities in the field that it could not be measured for volume and solute concentration. The nectar sugars of all species for which there are data are hexose dominant and have trace amounts of sucrose or none at all.

Insect pollination of bowl vs. stellate flowers. Bowl flowers are visited by a wide variety of insects, with short-tongued flies and scarab beetles predominant (Table 4). All insects observed on these bowl-shaped flowers land on the tepals and then crawl into the floral bowl. As they enter the flower, dorsal parts of the bodies of beetles, flies, and *Apis mellifera* brush against the anthers and stigma lobes. Beetles may remain at rest in the floral cup for at least 15 minutes with their heads lying against the base of the filament column and their abdomens or entire bodies visible from above. Of the 69 insects found to carry pollen of their host flowers (Table 4), 58% carried pure loads of the species on which they were captured.

The four species with stellate flowers are visited exclusively by bees in the families Apidae (*Apis mellifera*, *Anthophora diversipes*), Halictidae, and Melittidae (*Rediviva* spp.). Bees normally land directly on the anthers where they actively remove the pollen from dehisced anthers. After foraging for pollen some bees crawl onto the tepals and forage for nectar in the chamber at the base of the filament column. Of the 24 bees netted on stellate flowers and found to carry pollen of their host flowers (Table 4), only 6 individuals (25%) carried pure loads of the species on which they were captured.

While *Apis mellifera* forages for nectar and pollen on six species included in the study, field observation and pollen load analyses show that individuals foraged for pollen on co-blooming species including *Drimia* (Hyacinthaceae) and *Oxalis* (Oxalidaceae). *Anthophora diversipes*, collected on *M.*

miniata, carried pollen of *Gladiolus* sp. (Iridaceae), *Lachenalia* sp. (Hyacinthaceae), and *Lobostemon* sp. (Boraginaceae). *Rediviva* species, collected on *M. bifida* and *M. miniata*, also forage on co-blooming *Diascia* sp. (Scrophulariaceae) and *Oxalis* sp.

DISCUSSION

The columnar organization of the androecium and gynoecium in combination with the shape of the perianth of the nine species of *Moraea* studied shows a clear correlation with the major pollen vectors. Species with bowl-shaped perianths are pollinated primarily by insects that are more likely to consume nectar or pollen. Contact between the pollinator and the anthers and stigmas at the apex of the column is passive and dorsal. In contrast, the apex of the column of species with stellate flowers offers pollen as the primary reward to female bees, and contact is typically active and ventral (Bernhardt, 1996).

It is noteworthy that the flowers of *Moraea* species studied here produce hexose-dominant nectar in contrast to sucrose-rich to sucrose-dominant nectar found in the vast majority of the many species in several other genera of Iridaceae examined for nectar sugars (Goldblatt et al., 1995, 1998b; Manning & Goldblatt, 1996, 1997). Hexose-rich to -dominant nectar is found elsewhere in the Iridaceae only in species of subfamily Nivenioideae and some species of Ixioideae that have flowers adapted for pollination by sunbirds (Goldblatt, 1993). Hexose-rich nectar is commonly associated both with flowers pollinated by passerine (perching) birds and some insects with short mouth parts including certain flies (Baker & Baker, 1983, 1990). Most of the many members of Iridaceae subfamily Ixioideae so far examined for nectar chemistry, whether pollinated by short- or long-tongued insects, have sucrose-rich to sucrose-dominant nectar (e.g., Goldblatt et al., 1998a, b; van Wyk, pers. comm.), and the presence of hexose-dominant nectar appears to be the result of pollinator-driven selection. The difference in *Moraea* (subfamily Iridoideae) may simply be due to the nectar source, from perigonal nectaries in bowl-shaped or stellate flowers in contrast to nectar produced from septal nectaries in species of Ixioideae and Nivenioideae, rather than reflecting pollinator selection for a particular nectar type. Species of Ixioideae pollinated by short-tongued insects including andrenid bees, hopliine beetles, and tabanid flies consistently have sucrose-rich nectar.

Stellate or bowl-shaped flowers with prominent staminal columns in *Moraea* are specialized rela-

tive to the ancestral (plesiomorphic) condition in the genus, the *Iris*-like flower composed of meranthia (Goldblatt, 1990, 1991), and are closely correlated with a particular pollination system. The meranthium organization has been lost in some 60 of the estimated 195 species of *Moraea* (Goldblatt, 1981, 1986, 1991; Goldblatt & Manning, 1995), including those studied here, as a result of a complete structural reorganization of the floral parts that includes the reduction in size of the style branches, suppression of stigmatic crests, and loss of the close relationship of the outer tepal to its opposed style branch and stamen.

The mode of pollination in these species appears to depend primarily on shape and depth of the floral cup, and thus the degree to which the staminal column is exerted from the flower, and secondarily to the degree of coalescence between anthers in the column. These two architectural features determine whether anthers will swab the back of pollinators entering a flower in search of nectar or serve as a site of active pollen collection for polylectic bees. Both systems occur extensively within *Moraea* and also characterize the genus *Ferraria* (Iridaceae tribe Irideae) (de Vos, 1979), the ancestors of which have an *Iris*-type flower. Stellate flowers with the stamens and style arranged in a column in *Moraea* appear to reflect an unusual modification to exploit polylectic bees in a genus in which pollination by bees is ancestral but based on an entirely different floral organization. *Moraea bifida*, *M. miniata*, and *M. pseudospicata* are thus representative examples of several species in the genus that display a shift toward the evolution of a pollen flower derived from bilabiate, nectariferous ancestors. Pollen flowers are relatively uncommon in *Moraea*, and are derived in the genus. In contrast, floral evolution in *Moraea* species with bowl-shaped flowers appears to exploit a wide range of potential pollen vectors. These flowers often use scent as an attractant, offer visible nectar, and are pollinated by insects that may acquire pollen loads passively.

One of the more striking modes of floral convergence in the angiosperms has been in the evolution of stamens and carpels into columnar units. This occurs at two different levels. In such families as the Marantaceae, Fabaceae, Proteaceae, Polygalaceae, Meliaceae, and the orders Asterales, Campanulales, and Rubiales, part of the style or stigma becomes a pollen presenter or cup-like indusium (Kennedy, 1978; Ladd & Donaldson, 1993; Burns-Balogh & Bernhardt, 1985). In these flowers the anthers dehisce in the bud and empty their contents onto a sticky or hairy portion of the carpel. In the other example, most well known in the As-

clepiadaceae, Orchidaceae, and Stylidiaceae, flowers show true adnation between the androecium and gynoecium forming gynostemium or gynostegium (sensu Lawrence, 1951). The arrangement of stamens and style in the *Moraea* species with flowers like *M. pseudospicata* is intermediate between these two major columnar developments. Self-fertilization due to the close proximity of the anthers and pollen to the stigmatic surfaces is avoided by self-incompatibility.

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